

# HISTOLOGY OF APPLE FRUIT TISSUE IN RELATION TO CRACKING<sup>1</sup>

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## INTRODUCTION

Extensive loss often is incurred in the production of various fruits, notably sweet cherries (*Prunus avium* L.) and certain varieties of apple (*Malus sylvestris* Mill.), as a result of cracking of the skin and fleshy tissues sometime prior to harvest. Recent investigations have shown that in some of these fruits cracking is associated with abnormal acceleration of fruit growth or swelling as a result of a marked increase in water supply to the tissues. Verner and Blodgett (12)<sup>2</sup> found that cracking in sweet cherries was induced by an osmotic absorption of water through the fruit skin when this remained wet during prolonged periods of rain; and Verner (10) concluded that cracking in Stayman Winesap apples is promoted by increased water supply to the fruit tissues as a result of greatly depressed transpirational water loss under conditions of high humidity. In general, there seems to be a tendency for both cherries and apples to become increasingly susceptible to cracking as the fruits approach maturity.

Among different varieties of the same kind of fruit striking differences in tendency to crack have been observed. Bing, Lambert, and Napoleon sweet cherries are highly susceptible to this injury, while Republican, Eagle, and many other varieties are more or less free of it (9). Stayman Winesap apples sometimes crack severely, while apples of other varieties on nearby trees do not crack at all. Even among different individual fruits on the same tree remarkable differences in tendency to crack may be observed, some fruits cracking severely rather early in the season while others are still sound at maturity.

We may infer from such observations that some varieties, in general, and certain specific fruits of those varieties in particular, are in some manner peculiarly predisposed to cracking. Evidently those forces tending to promote unusually rapid swelling of the inner tissues through increased hydration are not alone responsible for this phenomenon. Some fruits, apparently, are able to accommodate these rapid rates of enlargement by corresponding growth or stretching of the peripheral tissues, while other fruits are not so adapted. The environmental influences that tend to promote cracking must, therefore, be regarded as merely contributory.

The present study was undertaken with the hope of finding a histological basis for the explanation of these diverse tendencies of different fruits to crack. Sections of fruit tissue of the highly susceptible Stayman Winesap apple were compared with similar tissues of several varieties in which cracking is rare. The latter varieties included Winesap, Winter Banana, Grimes Golden, Gano, and

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<sup>2</sup> Italic numbers in parentheses refer to Literature Cited, p. 823.

Arkansas. Especially careful examination was made of tissues adjacent to cracks in Stayman Winesap; and specimens of this variety that had cracked were compared with specimens which, although growing in the same orchard or on the same tree, had remained sound.

In a fruit such as the apple, which approximates a spherical shape, the most rapid growth in a tangential direction must occur in the outermost tissues. If growth or tangential stretching in these parts is unable to keep pace with growth or swelling of the underlying tissues (largely cortex in the apple), cracking may be expected to occur in the fruit periphery. The nature of tangential growth or stretching of the epidermal and hypodermal layers, roughly constituting the fruit "skin," is, therefore, of special interest in a study of cracking in this fruit. The relative positions of these tissues and the manner in which they are involved in cracking are shown by the photomicrograph in plate 1, *A*. Major consideration has been given to these tissues.

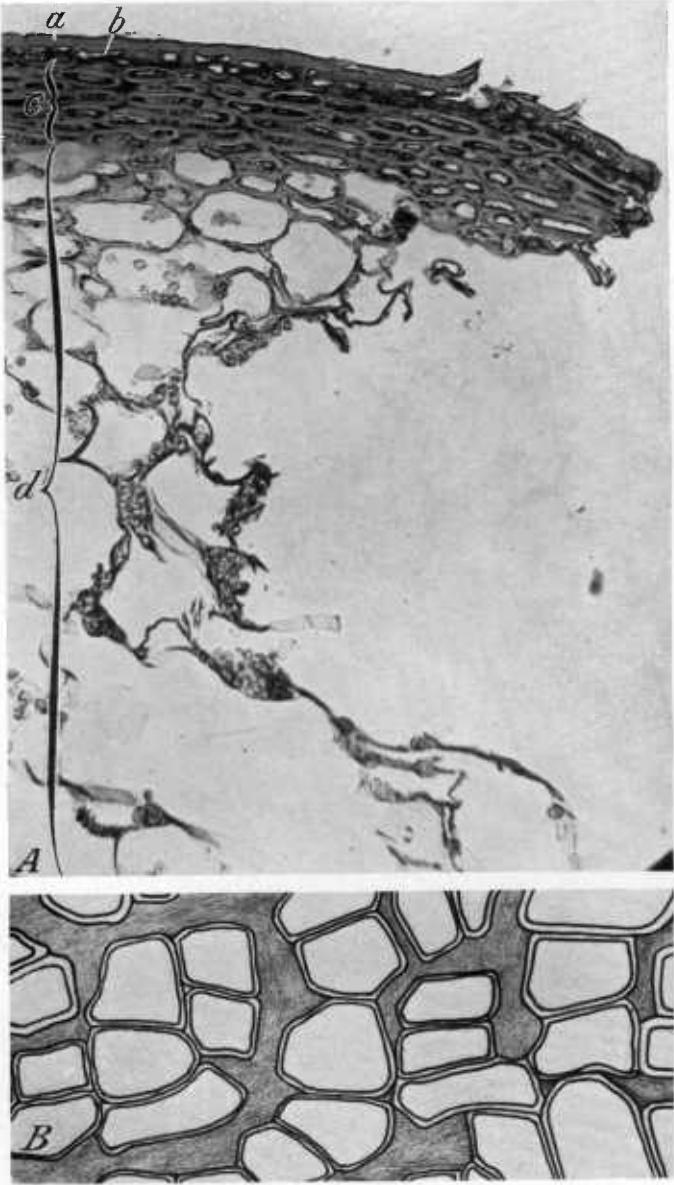
### REVIEW OF LITERATURE

Since a review of literature on the subject of fruit cracking has been published recently (10), only such papers as have a direct bearing on the present study are considered here.

Tetley (8), in an anatomical study of Bramley Seedling apple, found that both cell division and cell growth continued later in the hypodermal layer of cells than in any other part of the cortex; and epidermal cells, she states, may continue to divide as long as the fruit is growing. As a rule, however, cell division in these regions decreases with advancing maturity, and much of the tangential stretching to which the peripheral tissues are subjected late in the season seems to be accommodated by a change in the direction of the long axes of cells in this region. In very early stages of development, when the apple is newly "set," the epidermal cells are somewhat brick-shaped, with their long axes lying in a radial plane; but, as growth proceeds, these cells seem gradually to yield to stretching until, at maturity, their long axes lie in a tangential plane. In the hypodermal cells also the tangential dimensions increase more rapidly than the radial dimensions in the later growth stages. This change in shape of epidermal and hypodermal cells, as a result of tangential stretching, might conceivably provide for a considerable increase in surface area of the fruit without any appreciable cell growth having taken place.

Tetley states that the epidermis of Cox Orange Pippin, an English variety of apple that cracks readily, is characterized by deposition of cutin on the outer tangential, the radial, and the inner tangential walls of the epidermal cells. She considers that this type of cuticle offers less resistance to tangential stretching than a type of cuticle that covers only the outer tangential walls, or the outer tangential and radial walls of the epidermal cells. She seems to consider the type of cuticle of Cox Orange Pippin at least partly responsible for the tendency of this variety to crack.

Zschokke (13) observed that hairlike epidermal cells present in very young apples commonly are broken in the early growth stages of the fruit, leaving in the epidermis minute openings which subsequently become suberized and give rise to lenticels. Tetley (8), who also observed these hairlike structures, states that upon collapse of such turgid cells in a stretched epidermis small cracks in the skin may appear.



A, Transverse section showing one side of a shallow crack in a Stayman Winesap apple and the tissues involved in such cracking.  $\times 125$ . *a*, Cuticle; *b*, epidermis; *c*, hypodermis; *d*, cortex. B, Tangential section through epidermis of Stayman Winesap apple showing cut-in (shaded portions) deposited between groups of epidermal cells. Traced from a photomicrograph.  $\times 500$ .

According to Sorauer (7) cork formation usually occurs in the tissues subjacent to such small cracks, and this cork development may result in local russetting of the fruit skin. In subsequent growth of the fruit, cracks are likely to appear in such regions because of nonuniform swelling of the russet and the healthy areas.

Verner (10) considers that lenticel hypertrophy, which seems to be induced by the same environmental conditions that promote cracking, may sometimes constitute an initial stage in the development of cracks in Stayman Winesap apples. He points out that cracks in this variety occur most commonly in areas characterized by some abnormality of the peripheral tissues, such as russetting, lesions of apple scab (*Venturia inaequalis*), sunburn, or high skin coloration—conditions that seem to decrease the extensibility of these tissues.

Kertesz and Nebel (3), in a study of varietal differences in susceptibility to cracking in sweet cherries, found that those varieties that cracked most readily had smaller cells and thus, presumably, more cell-wall material than those resistant to cracking. When finely divided pulp of different varieties was placed on wet filter paper in funnels it was found that a relatively large percentage of the juice was retained by pulp of the varieties most susceptible to cracking, while in the noncracking sorts much of the juice passed through the filter. The greater retention of liquid by pulp of the varieties that crack badly was attributed to the imbibitional properties of the greater amount of colloidal substance in these fruits. These colloids of the cell walls, they conclude, probably exert a greater influence on absorption of water by the fruit in periods of rain than do the osmotically active constituents of the cell vacuoles; and they consider that varietal differences in colloid content serve to explain differences in their susceptibility to cracking.

#### METHODS OF PROCEDURE

The apple tissue samples used in this study were secured in 1933 and 1934 from nearly mature fruit grown at the Kearneysville Experiment Farm of the University of West Virginia. By means of a razor blade, wedge-shaped pieces of tissue were cut from the apple cheek in such a manner that each consisted of a 5-mm square of fruit skin and tapered on radial planes toward the core. In length these pieces of tissue ranged from 1 to 3 cm, the longer pieces usually traversing the cortex and including a portion of the pith of the apple.

As soon as a tissue sample was removed from an apple it was placed in a formalin-alcohol killing and fixing solution. The samples were prepared for embedding in paraffin by a routine procedure of dehydration in an alcohol series of increasing concentrations from 35 to 100 percent, and by clearing in a series of alcohol-xylol mixtures of increasing concentrations of xylol from 33% to 100 percent. Paraffin with a melting point of 52° C. was used for embedding. Transverse sections 10 to 15 microns thick were cut with a rotary microtome, and these sections were stained with Delafield's haematoxylin and Sudan III according to the schedule recommended by Baker (1). The stained sections were mounted in glycerin jelly.

Photomicrographs were taken by means of a euscope equipped with a camera attachment. Length of exposure of the plates was controlled

through the use of a camera shutter attached to the substage of the microscope. A carbon-arc lamp served as a source of light.

Most of the sectioning, staining, and study of these tissues was carried on in 1935 and 1936 at the University of Idaho.

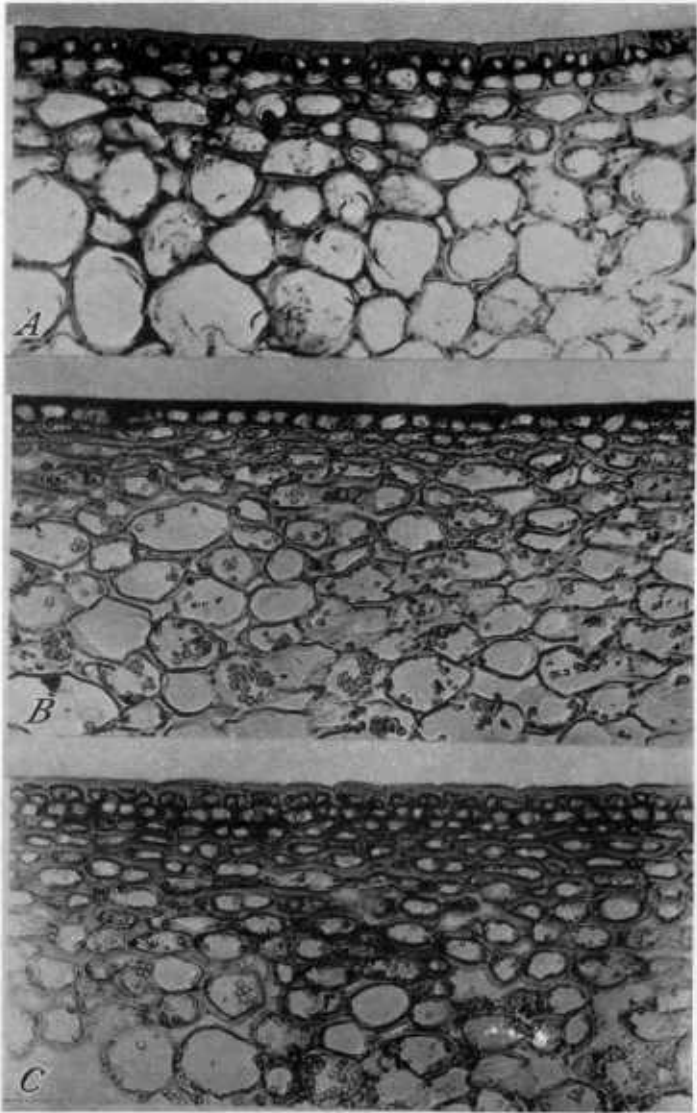
## OBSERVATIONS

### DIFFERENCES IN THE PERIPHERAL TISSUES OF CRACKING AND NONCRACKING APPLES

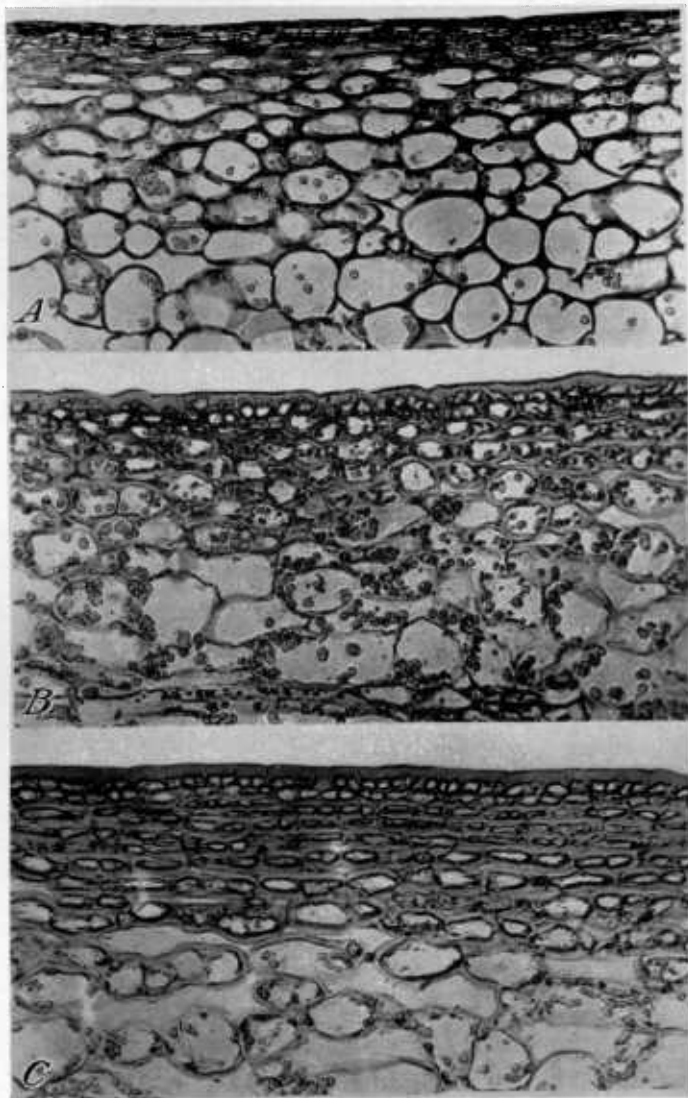
There were observed no consistent differences in structure of the cuticle or of the epidermis that might help to explain the tendency of some fruits to crack. In all varieties examined the cells of the epidermis had been pulled apart into small groups, as shown in plate 1, *B*, and the epidermis had remained intact only by virtue of increase in the cuticle, which had been projected into the interstices formed between the radial walls of cells that had been separated. In many cases cells of the epidermis were completely embedded in cutin and obviously were incapable of further growth. The development of this condition of the epidermis probably is attributable to premature cessation of division and growth in the cells of this layer, with a subsequent separation of these cells, one from another, as the epidermis is called upon to cover a larger and larger area of fruit surface. Preservation of the epidermal layer as a continuous, unbroken covering over the fruit is, therefore, dependent primarily upon continued deposition and stretching of the cutin that holds the epidermal layer intact. Since deposition of cutin may thus supplement deficient growth of the epidermis, the failure of the epidermal tissue itself to maintain an adequate growth rate cannot be regarded as contributing materially to the susceptibility of a variety to cracking. This view is supported by the fact that in varieties resistant to cracking, as well as in Stayman Winesap, the epidermis behaves in this manner.

In the hypodermal region of these apples striking differences were observed among the varieties studied, and these differences appear to be intimately related to the phenomenon of cracking. In Stayman Winesap the cells of the hypodermis, like those of the epidermis, showed unmistakable evidence of a deficient growth rate in the later stages of fruit enlargement; but this was not so of the varieties resistant to cracking. With few exceptions, the Stayman Winesap tissues examined were characterized by a more clearly defined hypodermal layer than was observed in any other of the varieties studied. In Stayman Winesap this layer consisted of much smaller and thicker-walled cells than were found in the subjacent part of the cortex, and these two regions usually were quite distinct. In most of the other varieties the hypodermal layer usually lacked a definite outline, the somewhat smaller cells of this region merging imperceptibly with the larger cortical cells. These different types of hypodermis are illustrated in plates 2 and 3, showing partial cross-sections of tissue from apparently normal fruits of Arkansas, Gano, Winesap, Grimes Golden, Winter Banana, and Stayman Winesap.

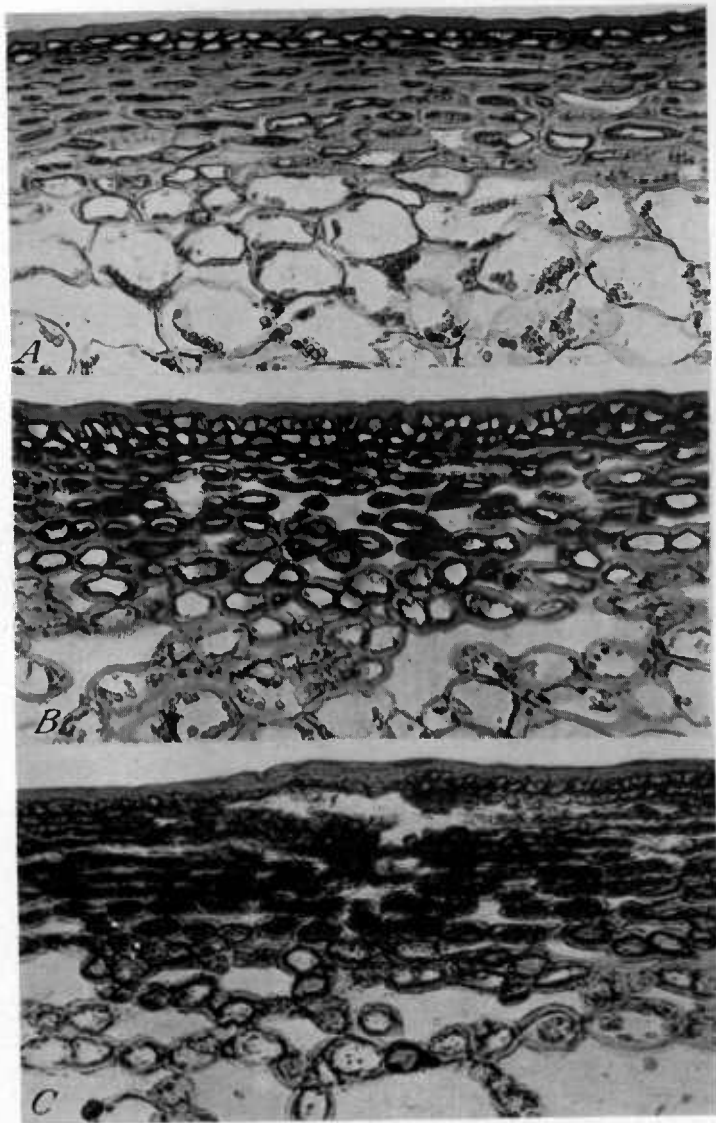
As shown in plate 3, *C*, tangential dimensions of the hypodermal cells of Stayman Winesap often are much greater than the radial dimensions, indicating that late growth of the fruit cortex was accommodated in the peripheral region principally by tangential stretching of the hypodermal cells rather than by cell growth. In the other



Transverse sections showing epidermal, hypodermal, and outermost cortical tissues of apple varieties resistant to cracking: *A*, Arkansas; *B*, Winter Banana; *C*, Winesap.  $\times 125$ .



Transverse sections showing epidermal, hypodermal, and outermost cortical tissues of apple varieties: *A*, Gano (resistant to cracking); *B*, Grimes (resistant to cracking); *C*, Stayman Winesap (susceptible to cracking).  $\times 125$ .

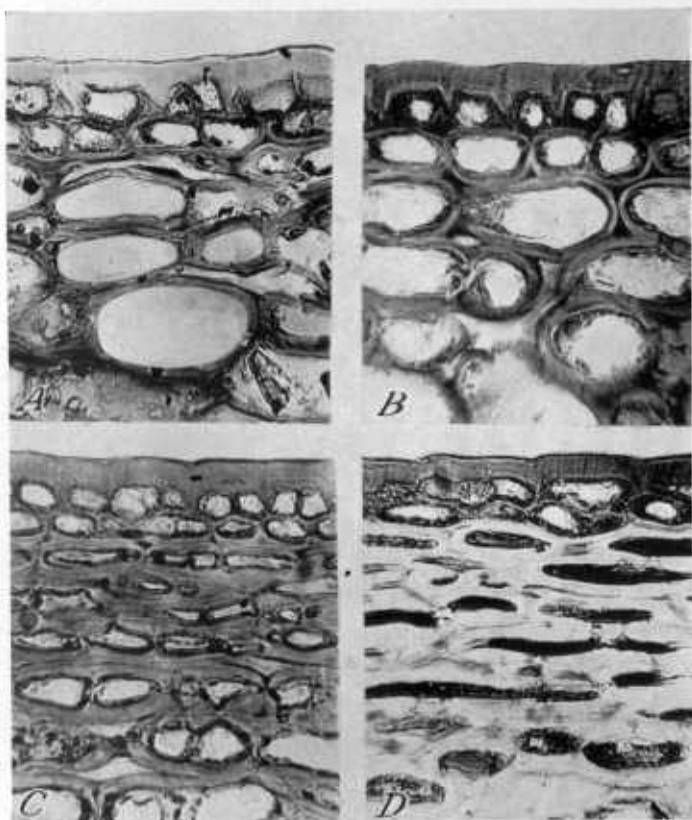


Transverse sections of Stayman Winesap apples showing modifications of normal peripheral tissues: *A*, adjacent to a crack; *B*, in a sunburned area; *C*, in an area probably injured by a lime-sulphur fungicide.  $\times 125$ .





Transverse sections of Stayman Winesap apples showing: *A*, tangential elongation of hypodermal cells under cork tissue (*a*, cork; *b*, cork cambium; *c*, hypodermis).  $\times 600$ . *B*, Hypodermal cells cut off from cortex by a deep layer of cork (darkly stained zone—*a*) and incipient cracking in the hypodermis.  $\times 125$ .



Transverse sections of epidermal and hypodermal tissues: *A*, of densely shaded, noncracking type of Stayman Winesap; *B*, normal fruit of Arkansas, a non-cracking variety; *C*, normally exposed but uncracked fruit of Stayman Winesap; *D*, adjacent to a crack in Stayman Winesap.  $\times 300$ .

photomicrographs of plates 2 and 3, representing varieties resistant to cracking, cells in the hypodermal regions are nearly isodiametric in cross-sectional outline and we may assume that, in these varieties, the rapid expansion necessary in the outermost tissues during the later stages of fruit enlargement was taken care of by cell growth.

Sections of Stayman Winesap tissue adjacent to or including a crack (pls. 1 and 4, *A*) show even greater elongation of the hypodermal cells than was observed in normal tissue of this variety. In many of these cells the lumen is almost closed as a result of tangential stretching or a combination of stretching and radial compression from the swelling inner tissues. Cells such as these appear to have reached their limits of extensibility, and further growth of the fleshy portion of the fruit without commensurate growth in the hypodermis might be expected to sever these tissues and result in a crack. The more rounded hypodermal cells of noncracking varieties might, without further growth but simply by tangential elongation, permit a considerable increase in fruit volume without being torn apart.

#### TISSUE MODIFICATION IN SUNBURNED, SPRAY-INJURED, AND RUSSETED APPLES

Plate 4, *B* shows tissue of Stayman Winesap in a region characterized by sunburn, a condition of the fruit commonly associated with cracking. The loosely knit structure of the hypodermal layer suggests that growth of the cells in this region ceased or was greatly restricted before growth of the fruit as a whole came to an end, the hypodermal cells, consequently, having been pulled apart. A similar condition, the cause of which is not definitely known, is shown in plate 4, *C*. This apparent injury of the subepidermal layers is thought to be of the same origin as that described by Baker (1) and attributed by him to the use of a lime-sulphur fungicide late in the growing season. This condition, like that associated with sunburn, seems to predispose the affected region to cracking. We find here a disintegration of both epidermal and hypodermal tissues that would preclude further growth in these layers. Subsequent expansion in response to continued fruit growth should lead to cracking in an area thus affected.

Tissue modifications that appear in the condition commonly referred to as russetting, and which greatly increase the susceptibility of an apple to cracking, are shown in plate 5. Such russetting, or cork formation, takes place following injury to the cuticle. A layer of cork cambium assumes the position normally occupied by the epidermis, cutting off to the outside several, or many, tangential layers of cork cells, which constitute the scurflike russet. In the sections of russeted fruit that were examined there was little evidence of the formation of phelloderm cells that usually are cut off to the inside by the cork cambium. Beneath the cork tissue the hypodermal cells often were much elongated tangentially (pl. 5, *A*) as in nonrusseted tissues adjacent to or including a crack (pls. 1, 4, *A*, and 6, *D*).

In many sections through russeted areas it was observed that a narrow band of cork tissue extended into and, at some points, beneath the hypodermal layer (pl. 5, *A*, *B*). Hypodermal cells so separated from the cortex often presented a striated appearance owing to tangential stretching, and this tissue was badly disrupted. Apparently growth

had been terminated in this region while the fruit still was enlarging, in consequence of which the cells first were stretched to the limit of their extensibility and then were gradually pulled apart. This would add to the roughness of these russeted areas, and it might lead to incipient cracking as shown in plate 5, *A*.

#### TISSUE MODIFICATIONS IN DENSELY SHADED STAYMAN WINESAP FRUITS

In 3 years of observation, sound, densely shaded Stayman Winesap fruits growing in the innermost parts of the tree were never found to crack. Upon examination such shaded fruits seemed always to have thinner skins than specimens from more exposed parts of the tree. Apples selected at random in different exposures on several trees and enclosed in brown paper bags from 3 to 4 weeks before harvest seemed also to have abnormally thin skins when they reached maturity, and the incidence of cracking in these bagged apples was much less than in fruits normally exposed. In 1932 there were only 5.2 percent of cracked apples among 210 that had been covered, while among 190 that had been tagged and left exposed, 41.0 percent had cracked.

Zschokke (13) states that apples of a variety normally russeted, if shaded early in the growing season, remained free of russet and were thinner skinned than unshaded fruits. Magness and Diehl (4) found with several different varieties that the skin on the cheek exposed to the sun was thicker than the skin on the shaded cheek. As shown in plate 6, *A*, sections of tissue of Stayman Winesap apples from densely shaded parts of the tree lack the clearly differentiated hypodermal layer seen in sections of exposed fruits of this variety. The hypodermal cells of these shaded fruits resemble those of varieties that are not susceptible to cracking. They are rounded in outline, they are not clearly distinct from other cells of the cortex, and they lack the stretched appearance of corresponding cells in more exposed specimens of the same variety.

*A* and *B* of plate 6 show the similarity in structure of the hypodermal regions of a densely shaded Stayman Winesap apple and a normal fruit of Arkansas, a noncracking variety; and these may be contrasted with *C* and *D*, showing, respectively, hypodermal tissues characteristic of normally exposed and of cracked Stayman Winesap apples. The close relationship between degree of tangential stretching of the hypodermal cells and cracking is clearly evident in these illustrations.

Darkly stained cell inclusions, as seen in plate 6, *D*, were observed commonly in tissues adjacent to or including a crack. The nature of these inclusions has not been determined, but it is suggested that they might consist of dead protoplasm and other contents of cells that were killed sometime before the fruit was picked. Upon the death of these cells their growth would, of course, be terminated, with the result that the cells would be elongated and compressed as growth continued in the underlying tissues. Similar inclusions were present in cells of sunburned tissue, as shown in plate 4, *B*, in which the dark intracellular masses are to be seen adhering to the walls of the cells. These cells, largely separated from the subadjacent tissue through which their nourishment had been derived, must surely have died sometime prior to picking of the samples. Had they been elongated and flattened as were those shown in plate 6, *D*, they would have pre-

sented much the same appearance as these, with slitlike lumina filled by the dark inclusions.

Plate 6 also affords a comparison of cell-wall thickness in cracking and noncracking specimens of Stayman Winesap. The much greater thickness of hypodermal cell walls in plate 6, *D* than in 6, *A*, is characteristic of all of the cracked specimens examined except those in which spray injury or russetting were involved. Not only are the cell walls of cracked specimens thicker than those of densely shaded fruits but, as a rule, they are thicker than those of normally exposed but uncracked fruits of the same variety.

The cell walls of hypodermal tissue in normal fruits of Stayman Winesap are not appreciably thicker than in normal fruits of Winesap, which is a variety highly resistant to cracking. We cannot, therefore, regard the thickness of hypodermal cell walls in fruits of Stayman Winesap as an inherent characteristic that bears a causal relationship to cracking. We may, however, consider that the unusual thickness of these cell walls in specimens of Stayman Winesap in which cracking has occurred constitutes a special form of tissue modification to which this variety is especially prone, and which, perhaps, contributes to the tendency toward cracking in such specimens.

#### DISCUSSION AND CONCLUSIONS

It appears from these observations of tissue structure that the high degree of susceptibility to cracking in Stayman Winesap apples is attributable primarily to a tendency toward marked restriction of growth in the hypodermal layer late in the growing season while the fleshy portions of the fruit may be enlarging at a normal or an excessive rate. Under average conditions, when enlargement of the fruit is proceeding moderately, this restricted growth of the hypodermal cells is supplemented by tangential stretching, and a combination of these two processes (growth and stretching) enables the hypodermal layer to expand sufficiently to keep pace with enlargement of the main body of the fruit. At the same time, the epidermal layer remains intact through a gradual stretching, and increase in quantity, of the cuticle in which it is partially embedded. Thus, when growth proceeds at a moderate rate the fruit seldom cracks; but under conditions of very high humidity and its attendant low transpirational water loss, when tissue hydration is increased and the rate of fruit enlargement is abnormally rapid (11), the limit of extensibility of the hypodermal tissue soon is exceeded and cracking occurs. Growth measurements taken at times when Stayman Winesap apples were in the process of cracking have shown (10) that many noncracking specimens enlarge at more rapid rates than those that crack. The phenomenon of cracking cannot, therefore, be attributed to an exceptionally rapid rate of swelling in the cortex of cracking specimens, but must be regarded as a result of inadequate growth in their peripheral tissues.

Incipient cracking frequently involves only the cuticle and epidermis, the rupture of which gives rise to cork cambium that soon replaces the normal epidermal covering with less extensible cork tissue, or russet, which predisposes the affected area to more severe cracking at some later time. In deeper cracks the epidermal and hypodermal layers may occasionally behave independently as shown in plate 4, *B* and *C*, where the epidermis remained intact when cells of the hypo-

dermal layer were pulled apart; but it is evident that, as a rule, these two tissues remain closely knit and behave as one in such cracking. To some extent the incapacity to maintain an adequate growth rate in times of abnormal growth acceleration in the deeper tissues seems to include part of the cortex below the hypodermis, since cracks commonly involve the cortex to a depth of 10 or more cells. As previously pointed out, the configuration of an apple is such that expansion of its tissues in a tangential plane during growth must be greater in rate as the issue in question is farther removed from the central axis of the fruit. It is to be expected, therefore, that in times of unusual growth acceleration other regions of the cortex may, like the hypodermis, become involved in cracking by reason of inability to maintain a growth rate commensurate to that of the underlying tissue.

There is a rather common view that cracking indicates lack of strength or resistance on the part of the fruit "skin" to withstand the pressure imposed on it by internal growth. Thus, Tetley (8), in discussing cracking in Cox Orange Pippin apples, states that the "epidermis was unable to resist the rapid swelling of the cells within and had consequently cracked." In view of the observations here reported it is doubtful whether we should look upon these outermost tissues of the fruit as offering any considerable mechanical resistance to expansion of the deeper tissues. At best, the epidermal and hypodermal layers combined constitute a covering not exceeding one-fifth of a millimeter in thickness, and in some varieties especially resistant to cracking, such as Arkansas and Winter Banana, no clearly defined hypodermal layer can be distinguished. Cracking, therefore, should be looked upon, not as evidence of failure of these outer tissues to repress an excessive growth rate but rather as evidence of their failure to keep pace with it. In other words, the problem of cracking in the apple involves inability of the peripheral region to stretch or to grow as rapidly as it should when the fleshy portion of the fruit is enlarging at an abnormal rate.

There is, of course, a considerable strain on these outer tissues as growth takes place, and when this strain becomes excessive, as it does when there is inadequate tangential growth or stretching, we may expect these tissues to be torn apart first at their weakest points. It has been observed in many instances that cracks in apparently sound tissue had their origin in hypertrophied lenticels. In lenticel hypertrophy there is a considerable extension of cork tissue beyond the normal limits of the lenticel. According to Eames and MacDaniels (2), cork tissue in most plants is both inextensible and inelastic. In an epidermis under great strain because of disproportionate growth of epidermal and cortical tissues such localized areas of inextensible cork would mark points at which the tissues might first be pulled apart. This role of lenticels in cracking of apples probably is not of great importance, however, if we assume that the antecedent cause of cracking lies in failure of the peripheral tissues as a whole to maintain an adequate rate of growth. In the absence of lenticels cracks might occur almost as soon in uninterrupted tissue. No data are available to show the percentage of cracks that originate in hypertrophied lenticels, but observation has shown that cracks frequently appear without relation to them.

The high incidence of cracking in parts of the apple affected by russetting, sunburn, scab lesions, and other skin injuries can be attributed directly to these abnormalities. Such modifications of the fruit periphery involve considerable areas in which extensibility of the tissues is below normal. This is demonstrated by the photomicrographs of sunburned, spray-injured, and russeted tissues in plates 4, *B* and *C*, and 5, respectively. In the first two instances the capacity for expansion of most of the tissue comprising the fruit skin has been prematurely halted by death of many cells in this region. In the case of russeted areas the tendency to crack has been aggravated by partial disruption of the hypodermal layer or by substitution of inextensible cork for the normal epidermal and subepidermal tissues. Freezing-point depressions of the cortex underlying these modified skin areas have been shown (10) to be appreciably higher than under normal skin. Thus, abnormal tissue pressures in the cortex combine with subnormal extensibility of the peripheral layers of cells in making these sunburned, russeted, and otherwise injured portions of the apple especially prone to crack.

We can only speculate as to the probable causes of the structural peculiarities that render exposed fruits of a susceptible variety of apple more likely to crack than others. It is known that exposure of plant tissues to direct sunlight increases transpirational water loss. Fruits most exposed to sunlight also are most exposed to wind and general air movement, which would tend further to remove water from their tissues. Cell growth, which can take place only when the cell is turgid, might thus be checked in periods of intense sunshine and high evaporativity, owing to a water-saturation deficit of the tissues. According to Palladin (5) a severe water deficit promotes thickening of cell walls in the affected region. Thus, the premature cessation of cell growth and abnormal thickening of cell walls associated with cracking in exposed parts of Stayman Winesap apples might be considered to result from the drying effects of their immediate environment. Under conditions of prolonged hot, dry weather, especially when accompanied by soil-moisture deficiency, all of the fruits on a tree might be affected in a similar manner, but in various degrees, as a result of inadequate water supply to the outer layers of cells. Such a hypothesis would serve to explain the common observation that cracking is most likely to occur and affects the largest percentage of the crop if an abundant moisture supply is made available to the fruit following a protracted period of water shortage.

Cessation or restriction of growth in hypodermal tissues underlying russeted areas (pl. 5, *A*), might be due to a prolonged water deficit resulting from excessive moisture loss through the overlying zone of cork, which, according to Baker (1), is much more pervious to water than is normal cuticle. When all or part of the hypodermal region is separated from the cortex and from contact with vascular elements by a layer of cork, as in plate 5, *B*, further growth of the hypodermal cells might be inhibited by reason of restricted passage of nutrients and water through the suberin-impregnated zone below them. Occasionally both the epidermal and the subepidermal tissues are completely replaced by cork. In all of these conditions associated with russetting the normal peripheral tissues have been replaced by tissues that are much less extensible and that, therefore, increase the susceptibility of the affected area to cracking.

There is no evidence indicating that the theory of Kertesz and Nebel (3) regarding the role of colloids in cracking of cherries is applicable to this phenomenon in apples. In all of the varieties studied the smallest cells and the thickest cell walls (therefore, the greatest proportion of colloidal cell-wall materials) were found in the outermost tissues of the fruit. Upon excessive absorption of water in this region a condition should be approached just the reverse of that which causes cracking; that is, there should be expansion of the peripheral tissues in excess of the requirements imposed upon these tissues by growth of the deeper-lying cortex. In the cortex, where an abnormal rate of swelling by absorption of water seems responsible for the tissue strain that promotes cracking, the proportion of cell-wall material to osmotically active cell contents is much smaller than in the outer tissues, because of the larger cell sizes and thinner cell walls in the cortex.

Although some water may be absorbed through the skin of Stayman Winesap apples in periods of rain (10), most of the water supply permeating the fruit in times of cracking seems to enter through the usual channels of the vascular system. If the cell walls of the cortex were able to imbibe this water and swell appreciably before the peripheral tissues had been able to expand proportionately by the same process, we might expect cracking to occur in somewhat the manner suggested by Kertesz and Nebel (3) for cherries. However, there is no reason for supposing that the deeper cortical tissues would have access to an increased flow of water in the vascular system very long before it reached the hypodermal layer, where, as pointed out, colloidal absorption and swelling would tend to prevent rather than to promote cracking. It has been shown (10) that detached Stayman Winesap apples, with stems and calyxes sealed with paraffin, may crack severely when they are held for a period of 48 hours under water. Thus, even when an increased water supply is made available first to the small, thick-walled cells of the outer tissues by absorption directly through the skin, relatively greater swelling takes place in the region of the larger, thinner-walled cells of the cortex, and cracking results.

There seems to be little basis for assuming that the colloidal constituents of the cell walls would play a more important part in swelling of the fruit than do the osmotically active constituents of the cell vacuoles. As pointed out by Shull (6), cell solutes and the colloids of the cell wall are approximately in equilibrium with respect to the degree in which their water-saturation deficits are satisfied. Therefore the water-absorbing powers of the cell colloids should not appreciably exceed the osmotic value of the cell solutes at any given time. Although, as Kertesz and Nebel (3) point out, some colloids may exert an imbibitional force of as much as 2,000 atmospheres, such high values apply to colloids in a dry, or nearly dry state, whereas in the flesh of a fruit such as cherry or apple the actual colloidal pressure must be only a small fraction of its potential pressure due to the degree of hydration that exists in such succulent tissues. It is more likely that the excessive swelling of the fleshy portion of the fruit in times of abnormal water supply is due to the combined hydration forces of all those constituents of the cell and cell wall that tend to draw water to themselves, including both colloidal substances and cell solutes, which are component parts of the same equilibrated system.



## SUMMARY

Different varieties of apple, and different individual fruits within a variety, exhibit striking differences in tendency to crack under the same environmental conditions. In an attempt to find a histological basis for the explanation of such differences fruit tissues of Stayman Winesap, a variety highly susceptible to cracking, and comparable tissues of five varieties usually immune, were sectioned and stained for microscopic study.

In most of the sections of Stayman Winesap that were examined, and especially in tissues in which cracking already had occurred and in those characterized by certain abnormalities commonly associated with cracking, there was definite evidence of premature cessation or retardation of growth in the peripheral tissues. In the epidermis the cells had been separated into small groups and the intervening spaces were filled with cutin, which thus preserved the continuity of the epidermal layer. This condition of the epidermis was evident in both cracking and noncracking varieties, however, and the structure and growth habit of the epidermis are not considered of great importance in determining the degree of susceptibility of a variety to cracking.

In Stayman Winesap the hypodermal layer of cells likewise showed clear evidence of an inadequate growth rate late in the season, as these cells were much elongated tangentially, suggesting that recent enlargement of the fleshy portions of the fruit had been accommodated in the hypodermis primarily by tangential stretching. In noncracking varieties the cells of the hypodermis were nearly isodiametric in cross-sectional outline, and evidently had maintained a growth rate proportional to that of the underlying tissues.

On the basis of these investigations there is advanced a hypothesis that the susceptibility of Stayman Winesap apples to cracking is due chiefly to premature cessation or restriction of growth in the hypodermal layer. Upon unusual acceleration of growth in the fruit cortex, as under conditions of very high atmospheric humidity with its attendant increase in tissue hydration, the limit of extensibility of the hypodermal layer soon is reached and further expansion of the tissues beneath leads to cracking. The phenomenon of cracking, therefore, probably should be regarded, not as a result of failure of the peripheral fruit tissues to repress an excessive growth rate of the cortex but rather as a result of their failure to keep pace with it.

This premature retardation of growth in the hypodermal layer seems to be related in some manner to exposure of the fruit to sun and general air movement, as the condition is greatly accentuated in tissue so exposed and is virtually absent in tissues of densely shaded fruits. Abnormal susceptibility to cracking in sunburned, spray-injured, and russeted areas is due to special types of structural weakness in the parts involved.

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